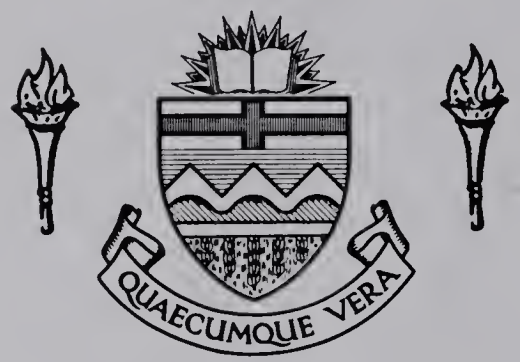

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THE EFFECTS OF SEPTAL LESIONS ON FACTORS OF MOUSE EMOTIONALITY

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© RUTH LUKAWESKI

A THESIS

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ABSTRACT

This experiment was designed to investigate the effects of septal lesions on factors of emotionality in two emotionally divergent strains of mice, Balb/Alb and C57/Alb. It was decided to use a 2 x 2 x 3 x 5 factorial design to measure the main effects of strain, sex, lesion type (septal, control and operate control) and days of testing. Sixty mice were obtained from the University of Alberta, Edmonton, allotted to their proper groups and then tested on a factor analytic battery of 19 measures of emotionality. Six factor scores were derived and analyzed according to the planned analysis of variance design. Two factors, Factor II (Motor Discharge) and Factor VIII (Autonomic Balance), showed main effects attributable to septal lesion. Significant interactions were found between lesion and strain for Factors II and V (Tunneling 1), and between lesion and sex for Factor IX (Territoriality). The results support the hierarchical model of emotional arousal proposed by Royce.

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Chapter 1. Introduction.

A twelve-year program of multivariate research at the University of Alberta has uncovered several invariant factors of emotionality in mice (Royce, Carran and Howarth, 1970, Royce and Poley, 1973, Royce, Poley and Yeudall, 1973). There are many reasons for adopting multivariate methods in the comparative and physiological domains and in the study of human individuality (Royce 1950, 1966, 1973). In the study of animal emotionality factor analysis has some notable advantages. It prevents premature closure on the concept of emotionality itself and its putative measures. It provides the maximum opportunity for intuitive distinctions in the area to manifest and verify themselves in empirical data-patterns while functioning as a generator of theoretical constructs in its own right (Royce, 1963). And once some invariance has been achieved, it greatly increases the precision with which univariate and bivariate research can be brought to bear on the determinants of emotionality. For factor analysis can distinguish more than one valid referent for the term 'emotionality', and can thus raise its questions and, hopefully, present its answers factor by factor, with obvious gains in clarity.

The method has been used to make some important contributions to the theory of emotional arousal in mice. By using a combination of factor and diallel analyses, it has been possible to present the genetic determinants of emotionality in much greater detail than was previously possible (Royce, Poley and Yeudall, 1974, Royce, 1973). A wide range of environmental determinants have been dealt with in similar

fashion, including infantile stimulation (Mos, Royce and Poley, 1973), light conditions (Vriend, Mos and Poley, 1974), litter-size (Egan and Royce, 1973) and alcohol intake (Poley and Royce 1973). The present study will deal with the effects of septal lesions on emotionality. As was the case in the studies just mentioned, our concern will not be to verify the phenomenon itself so much as to clarify it and draw out its theoretical implications by situating it in a multifactor theory of emotionality. Unfortunately, existing research on septal lesions cannot be directly reworked to this effect since the meagre amount of testing commits the data, irrevocably, to a uni-dimensional concept of emotionality. In other words, previous research has been content to describe septal emotionality in such simple terms as 'more' and 'less'.

It is the presence of this intuitive concept of emotionality which makes the literature on septal lesions difficult to interpret and, in our opinion, inconclusive in principle. At one time the concept of emotionality is understood narrowly and defined operationally by means of some standard test, such as activity or defecation in the open field. But at other times the concept becomes so broad that observed patterns of nest-building or social aggression are presented, without argument, as indices of emotionality. Thus it becomes impossible to say if the conclusions offered concerning the septum and emotionality are in agreement with each other or whether they are in disagreement - or whether, indeed, they are even relevant to each other.

Nonetheless, the <u>general</u> description of septal emotionality poses no problem. There is good agreement that the septal

animal is hyperirritable, aggressive, difficult to handle, and has an exaggerated startle response, sometimes to stimuli that were previously neutral (Brady and Nauta, 1953, 1955, Schwartzbaum, 1966, Pubols, 1966, Schwartzbaum, Green and Beatty, 1967). In fact, the general condition is so distinctive that it is sometimes referred to as 'septal rage' or 'the septal rage syndrome'.

But agreement ends as soon as analysis and quantification begins - a paradoxical situation which, in itself, casts suspicion on the methods being used. The most frequently used measure of emotionality in the septal literature is activity under stress. But the data here is equivocal, as Fried (1972) has already noted. In the open field Schwartzbaum and Gay (1966) and Corman, et al. (1967) report a decrease of activity in septals, while Donovick and Wakeman (1969) report an increase. Again, less activity is reported for septals in running-wheels and home cages (Clody and Carleton, 1969, Douglas and Raphelson 1966, Gotsick, 1969, Nielson, McIvor and Boswell, 1965; Thomas et al. 1959); but an increase in activity is reported for the same animals in mazes and novel environments (Nielson et al. 1965, Thomas et al. 1959; Corman, Meyer and Meyer, 1967, Gotsick, 1969). As some of these authors are well aware, the trouble here concerns the factorial complexity of the tests used. They have tried to meet this problem at the intuitive level by distinguishing between 'environments which are conducive to exploration' and others which are not, implying a similar distinction on the response dimension. While these authors raise the key issue, it is futile for them to attempt to deal with it given the data at their disposal. Conversely, as we hope to show, the

methods followed in this study readily handle the problem of 'impure' tests and derive all distinctions on the response dimension from the data at hand.

Next to activity, the other most-used test in the septal literature is urination and defecation under stress. Septal animals are reported to score higher than normals on these measures in standard open field apparatus (Nielson, McIvor and Boswell, 1965) and in a variably illuminated open field (Donovick and Wakeman, 1969). Apart from the variability in the test situation, it is clear that in these studies, as in others (King, 1958, Clarke, Meyer, Meyer and Yutzey, 1967) urination and defecation were only casually observed rather than systematically studied. This, however, is a small problem by comparison with the question of factorial complexity, which is especially bothersome in the case of urination and defecation measures because research at the University of Alberta has shown that urination tests consistently decompose into separate factors, one interpreted as Autonomic Balance and the other interpreted as Territoriality (Royce, Poley and Yeudall, 1973). Moreover, Territoriality has been connected with aggression (Egan, Royce and Poley, 1973), which in turn is an apparent characteristic of the septal animal. It is expected, therefore, that the present study will be able to present the urination and defecation measures of septal animals in a more meaningful fashion.

The literature is even more difficult to interpret when one moves on to other alleged expressions of emotionality. Maternal behavior is reported to be disrupted in mice with septal lesions (Carlson and Thomas, 1968) while sex-related

social behavior is increased (Michal., 1965). There is increased social aggression, with the expected adrenal hypertrophy (Montgomery, 1968). Septals also behave differently in conditioning tests. They do not show the usual freezing in response to cues for shock, they are better than controls at avoidance learning, and they endure large numbers of shocks to obtain water (Kaada et al. 1962). Frequently, however, the interpretation of such data is highly problematic. The conditioning patterns just described are claimed to be 'independent of hyperemotionality' on the grounds that the conditioning-pattern occurred without the overt symptoms of 'septal rage' and persisted even when the rage syndrome had disappeared. Consequently, the conditioning behavior itself was explained as a form of perseveration not involving emotional components (McCleary, 1966, Gerbrandt, 1965).

This, again, is the sort of theoretical issue which we hope to handle more adequately in the present study. The factor analytic approach allows the concept of emotionality to generate its own boundaries and its own internal structure. Intuitions about the 'emotional components' of a particular response, on the one hand, or about its 'independence' from emotionality, on the other, are replaced by a painstaking selection and modification of tests and, above all, by the elimination of tests which are found, on statistical grounds, to make no contribution to the sub-domain of emotionality. The current research program is many years past the point where intuitions such as the above have to be taken seriously. The present study, therefore, will not be concerned with demarcating the concept of emotionality or discovering its internal structure. This work is already available to us

from previous research. We will simply choose a subset of factors of emotionality reported in Royce et al. (1973) on the grounds of their invariance via a relatively small sub-battery of tests and their prima facie relevance to the special case of septal emotionality. The factors are Motor Discharge (II), Acrophobia (III), Tunneling 1 (V), Autonomic Balance (VIII), Territoriality (IX) and Tunneling 2 (XI). Simply stated, the purpose of the study is to re-examine septal emotionality in the context of this factor-structure in order to clarify the phenomenon itself and, thereby, achieve a more analytic understanding (i.e. in terms of psychologically functional components) of the function of the septum in emotionality. The septum, which is a major component of the limbic system, has long been implicated in emotionality. (For reviews of the literature, see Royce 1966, 1973). Though the limbic system will be a central topic in all future theories of emotional arousal, there are still major problems in setting the boundaries of the system itself and in locating the cortical/subcortical division within it (Royce, 1973, p372). More important, the role of the separate components of the limbic system is still virtually unknown. The hope of the present study is that a six-factor profile of septal emotionality will make a contribution to the role of the septum. More specifically, it should tell in what way it might be possible to think of septal function as relatively independent of other brain-functions. (For instance, Gray (1971) has proposed a model in which the septum would function as an inhibitor in emotional arousal, with the amagdyla controlling fight/flight systems and the hypothalamus controlling approach-systems). That is, it should give us some information as to what this function might be.

A final complication must be mentioned before commencing the method section. This concerns the time-dimension of our data-matrix. Since mice show rapid habituation to mild stress, current test-procedure is to average over two consecutive days of testing. However, septal emotionality is subject to habituation effects of its own. That is to say, the gross manifestations of septal rage tend to disappear post-operatively and complete disappearance has been reported after 21 days (Clarke, Meyer, Meyer and Yutzey, 1967, Yutzey, Meyer and Meyer, 1967) after 42 days (Kenyon and Krieckhaus, 1965), and after 70 days (Thomas and Kenyon, 1964). Moreover, there is evidence that the size of the lesion is the main determinant of the rate of habituation. These findings have been verified for mice by Slotnick and Jarvik (1966) and Slotnick and Brown (1970), who noted habituation after 10 days in mice with lesser lesions. In the present study it was decided to test on five consecutive days instead of two. This was partly to obtain some information on habituation. But it was also done to increase test reliability, for the exaggerated startle reflex of septals tends to give extreme scores on the first day of testing (they disappear on subsequent days).

Chapter 2. Method and results.

METHODS

SUBJECTS

60 mice from two emotionally divergent strains, BALB/Alb and C57/Alb were obtained from the University of Alberta, Edmonton. Upon arrival the animals were housed individually in steel cages and had food and water available at all times even during testing. Overhead flourescent lights were on a timed cycle; the room was illuminated between 9:30 a.m. and 9:30 p.m. 18 animals usually arrived at once and they were allowed two free days after arrival to get used to their cages. On the third day the animals were randomly allotted to their groups and the surgical procedures were begun. 4 animals were allotted to the control group, 4 to the operate-control group and 4 to the septal group. 4 extra animals were allotted to each of the operated groups to account for any losses or casualties from the operation or improperly placed lesions.

TESTS AND MEASURES

Open Field, Straight away and Pole.

Subjects were given one trial on all the tests on each of five consecutive days. The open field was a flat white masonite circle. 4 ft. in diameter with a 12 in. sheet metal wall. The field was divided into four annuli by scribing circles with diameters of 34 in., 20 in. and 6 in., using 4 cm. black lines. The two peripheral annuli were each divided into 16 equal portions by lines 14 in. apart. The next annulus was divided into eight equal portions leaving

a 6 in. circle in the center of the field. Two fluorescent lamps of 330 watts each were fixed 4 ft. above the field. The flat surface of the field was covered with a transparent plexiglass sheet. The entire apparatus was housed in a structure of 3/8 in. plywood, 64 in. long by 52 in. wide by 60 in. high with a one-way glass window 17 and 1/4 in. x 14 and 1/4 in. on one side and a door through which the experimenter entered on the adjacent side. S was placed in a small starting compartment in the outer annulus, the bottom was removed and the compartment was lifted by nylon strings from outside the housing. The following measures were taken for each two minute trial: latency to leave the first section (variable 1), number of lines crossed (variable 2), number of annuli crossed (variable 3), number of defecations (variable 4), and urinations (variable 5).

The straightaway apparatus consisted of a runway 50 in. long, 1.5 in. wide and elevated 31 in. above the floor. The runway was divided by .125 in. black lines into 11 interior sections 3.75 in. long and 2 sections 2.88 in. long at either end. It was illuminated by pink fluorescent lights behind opal glass, providing a uniform illumination of 20 ft. candles at the surface of the platform. The apparatus was housed in 3/8 in. plywood, 62 in. long 14 in. wide and 56 in. high. S was removed from its home rage and placed in a portable starting compartment which in turn was placed on the center section. The slidong bottom was removed and the compartment taken away. Observations made through the one-way window during a 3 min. trial were: Patency to leave the first section (variable 6), lines crossed (variable 7), number of fecal boli (variable 8) and urinations (variable 9).

In the Pole test, S was placed on a wire mesh platform on top of an aluminum pole. A wire mesh ladder on the pole made it possible to descend. The pole was 9 in. high, mounted on a 6 in. square metal base with a .125 in. mesh platform (1.5 x 2 in.) and ladder to the bottom. The pole was housed in a plywood observation box (51 in. high x 20 in. wide by 16 in. deep). Pink fluorescent lights illuminated the pole at 20 ft. candles. The measures recorded were: latency to remove all four feet off the platform (variable 10), time to descend (variable 11), number of fecal boli (variable 12) and urinations variable 13).

Cell and Hole-in-the-Wall. This apparatus was automated and made usable for either test by interchanging opaque and transparent top covers. The apparatus consisted of a wooden box, 26 in. long by 9 in. high by 4.5 in. wide, with three cubicles on each side 4 in. by 4 in. by 3 in. high. Each cubicle opened into a cubicle opposite and there was a black sliding door separating them. One set of 3 cubicles was covered with clear plexiglass and the other with opaque black plastic. The entire apparatus was housed in a 3/8 in. plywood structure 29 in. long, 42 in. wide and 22 in. high. The apparatus was illuminated by two 100 watt bulbs placed 16 in. apart at a distance of 10 in., above the apparatus. In Cell, the animal went from a dark compartment to a bright one and vice versa for Hole. S was placed in one of the cubicles with the sliding door closed. The door was opened and when S has moved all four paws over the threshold the appropriate timer was turned off. The measures recorded were: Cell, latency to emerge (variable 14), fecal boli (variable 15) and urinations (variable 16); and similarly for Hole (variables 17, 18 and 19).

It should be noted that all five tests were administered on the same day for five consecutive days and the order of the tests was never changed so that any dissipation of post-operative septal effects would confound a study involving different tests over a number of days. Administration of 5 tests on one day over 5 consecutive days increases the reliability of the results while any changes over days would suggest habituation effects due to practice. Unfortunately it might be hard to differentiate between habituation and dissipation of hyperirritability but the evudence suggests that it usually takes much longer than 5 days to wipe out hyperirritability.

DESIGN

19 measures of emotionality were selected from the battery currently in use at the University of Alberta (Royce, Poley and Yeudall, 1973). This was judged sufficient to yield the same factors found in previous research. Factor scores were computed on the six factors obtained by the formula $F=A'R^{-1}Z$ where A is the n x m factor structure matrix, Z is the n x N matrix of standard deviation of 10 were used. The factor structure used for this purpose was obtained from Royce, Poley and Yeudall (1973). Because of the large N in this study (775) this was considered to be the most reliable matrix available.

The obtained factor scores were analyzed in a balance 2 x 2 x 3 x 5 repeated measures design. The main effects and corresponding interactions under study were 2 strains by 2 sexes (males and females) by 3 lesion types (control, operate control and septal) by 5 days.

SURGICAL PROCEDURES

Animals were anesthetized with nembutal (60 mg./kg., I.P.). When surgical anesthesia was achieved, the animals were inserted onto the ear bars of the stereotaxic apparatus. The dorsal part of the skull was exposed. Co-ordinates used for septal lesions were: frontal, 1.0 mm. anterior to the anterior-most crossing of the sagittal and coronal sutures comprising bregma and/vertical 3.2 mm, below the surface of the skull. A mouse atlas is currently available but the coordinates used in this study were obtained from previous studies conducted in this laboratory. They are similar to the coordinates used by slotnick and Brown (1970) but strain differences had to be taken into account. A small hole was drilled at the desired spot with a dental drill and the electrode was inserted into the brain. Lesions were produced by passing a 2ma. anodal current to the brain for ten seconds through a stainless steel electrode insulated except for 1 mm. of the tip. Only one electrode was used per four animals. The scalp incision was closed with suturing thread and the wound was treated woth Neosporin antibiotic ointment.[1] Clean surgical procedures were observed throughout. The casualty rate was much lower than expected. Weights were taken immediately before surgery and right after testing. The only special post-operative, precautionery measure that was taken was keeping the animals warm with a portable heater. This seemed to guarantee a better recovery rate.

POST-OPERATIVE RECOVERY TIME

Since emotionality was the septal effect under study, it was decided that a 5-day postoperative recovery period would allow us an opportunity to study any manifest gross behavioral effects.

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[1]Sham control animals also underwent this procedure but no current was passed through the electrode

HISTOLOGICAL PROCEDURES

The day after termination of the experiment, the experimental animals were killed under deep anesthesia by intercardiac profusion of physiological saline followed by ten per cent formalin. The brains were fixed in 10% buffered formalin with 107 gum acacia added. The tissue was set in paraffin, sliced at 15 microns and every tenth section mounted. A combination stain was used luxol Fast Blue for the myelin and cressyl violet for the cells. All histological procedures were done by the histologist employed by the Psychology Department.

Lesion evaluation

For a good septal lesion, the area of damage should be bounded laterally by the lateral ventricles, dorsally by the corpus callosum and extends ventrally to the level of the anterior commissure. The lesions were evaluated by measuring the area of each septum on an appropriately traced drawing of the cross-section of the brain (see Figure 9). Then the area of the lesion damage to each septum was measured and the precentage of septum ablated was obtained by dividing the area of the lesion by the total volume of the septum.

Results

The lesions were a bit high in most cases and extended above the corpus callosum into the frontal neocortex. Most of the damage was done to the lateral nuclei of the septum rather than the medial nuclei which are located further down. The average amount of damage to each septum was 67% damage. Table 2 shows the % damage for each mouse brain (except mouse # R032). Individual photographs and drawings were taken of a choice section of the brain. These are presented in Figures 8 and 9.

BEHAVIORAL DATA:

The emotionality profile for all groups is plotted in Fig. 7. (Mean factor scores are in Table 11). It is immediately apparent that animals with septal lesions score considerably lower than the two control groups on Motor Discharge (II) and Autonomic Balance (VIII) while scoring close to normal on all other factors. The two differences noted are significant at the .01 level. The results are now presented in more detail.

MOTOR DISCHARGE (II) See Table 3 and Fig. 6a.

There is a significant main effect for lesion ($F=23.76$, $df=1/48$, $p<.01$). The mean factor score for septals is 44.54 as compared with 51.42 and 53.34 respectively for normal controls and operate controls.

There is also a significant main effect for strain ($F=53.35$, $df=1/48$, $p<.01$) and a significant lesion x strain interaction ($F=3.72$, $df=2/48$, $p<.05$). (See Figs. 1 and 2)

Finally, septals show a significant linear decrease on Motor Discharge over the 5 days of testing ($F=4.95$, $df=4/200$, $p<.01$). This is plotted in Fig. 6a.

ACROPHOBIA (III) See Table 4 and Fig. 6b.

The only significant finding for this factor was in the lesion x strain interaction ($F=3.46$, $df=8/200$, $p<.01$). The trend for days is plotted in Fig. 6 b and is significant ($F=6.27$, $df=8/200$, $p<.01$)

TUNNELING 1 (V) See Table 5 and Fig. 6c.

There was a significant strain x lesion interaction for this factor (F=5.13, df=2/48, p .01). This interaction is plotted in Fig. . There is also a significant trend over days (F=5.81, df= 4/200, p .01) which is plotted in Fig. 6c.

AUTONOMIC BALANCE (VIII) See Table 6 and Fig. 6d.

This factor showed main effects for lesion and strain (F=81,96, df=2/48, p .01; F=13.10, df=1/4, p .01). The septal group had a mean factor score of 45.76 compared to 53.33 and 50.91 for normal controls and operated controls respectively. The strain difference corroborates the profiles reported in Royce, Poley and Yeudall (1973) with the C57 strain scoring 47.30 as against 52.70 for the Balb strain. There was also a significant trend over days (F=3.80, df=4/200, p .01). When it is plotted (Fig. 6d) this trend produces an S-shaped curve.

TERRITORIALITY (IX) See Table 7 and Fig. 6e.

This factor shows a main effect for sex, with males scoring highest. (F=9.16, df=1/48, p .01). There is also a significant lesion x sex interaction (F=3.92, df=2/48, p .01) which is plotted in Fig. 5. The trend for days, which was not significant, is plotted in Fig. 6e.

TUNNELING 2 (XI) See Table 8 and Fig. 6f.

The only significant result obtained for this factor is for "trend over days" (F=3.60, df= 4/200, p .01). These findings

are plotted in Fig. 6f.

Chapter 3. Discussion

The effects of septal lesions on emotionality may now be stated precisely: emotional arousal is changed dramatically on two dimensions while remaining approximately normal on four others. The two dimensions affected are Motor Discharge (II) and Autonomic Balance (VIII). We will now discuss these behavioral findings and attempt to clarify the possible neural mechanisms involved.

Past research suggests that the medial and lateral nuclei mediate motor and autonomic reactions respectively. More specifically, the main function of the medial septal area is the generation of hippocampal theta waves (Low Voltage, Fast Activity) while the lateral septal area is mainly responsible for decreased autonomic activities because of its suppressing influence on the Reticular Activating System. Motor Discharge (II) is identified primarily by the latency, activity and penetration measures of the open field and the latency and activity measures of the straightway (see Table 1). The low scores of septals on this factor, therefore, are associated with longer latencies, less activity, and less penetration - findings which are in general agreement with those reported by Schwartzbaum and Gay (1966), Corman et al (1967), Donowick and Wakeman (1969) and Neilson, McIvor and Boswell (1965). Though the interpretation of activity factors of emotionality is not a simple matter (see Royce 1966, pp 675 f, for a discussion of the early literature), there is now little doubt that the constellation of low scores just referred to reflects less motor discharge - that is, a tendency to freeze in response to stress. It may be thought of as a state of tension or rigidity in the motor system, analagous to the

more obvious immobilization of Acrophobia (III). The first result of our study is that there is a decrease of motor discharge (or, conversely, an increase in freezing) in animals with septal lesions.

The second important result of this study is a clear decrease in another mode of emotional expression. Factor VIII is identified by defecation measures in a variety of test situations (see Table 1) and like any other factor, its interpretation has become clearer only with the accumulation of research (c.f. Royce, 1966, p667). This constellation of scores is now thought to reflect a tendency to express emotional arousal in an internal or visceral mode, via the autonomic nervous system (see Royce, 1973, p 328). The present study shows septals to be low on this form of emotional reactivity, a result which, to our knowledge, has been a source of controversy in the literature previously. It is contrary to the observations of Neilson, McIvor and Boswell (1965) and Donowick and Wakeman (1969), but consistent with the findings of Brady and Nauta (1953).

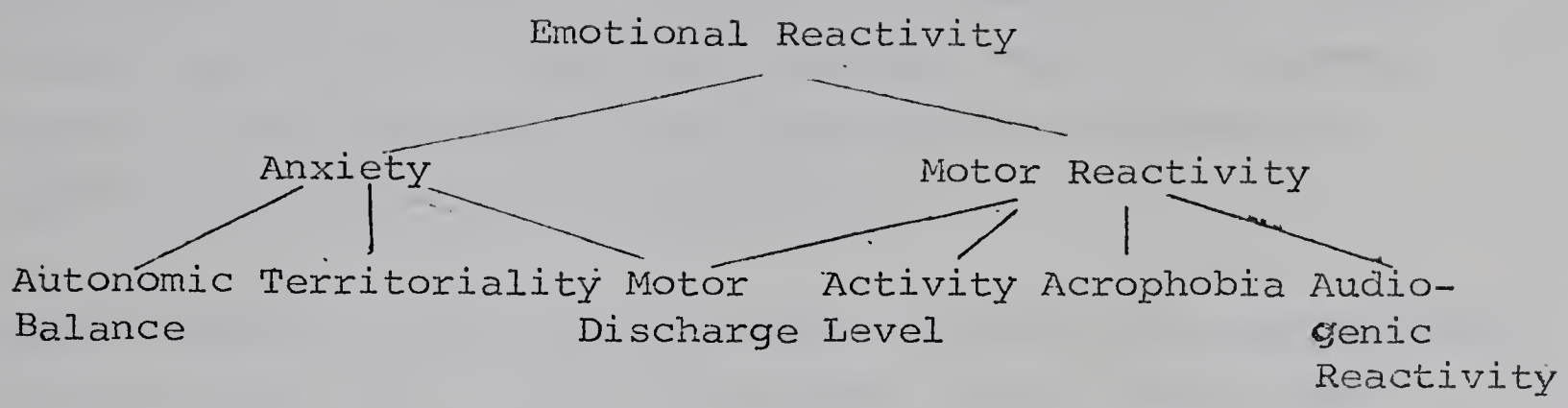
Although previous research has implicated the septal region as a mediator of emotionality, little has been said concerning the differentiation between the medial and lateral septal areas. As mentioned previously, the medial septal area is mainly responsible for neo-cortical desynchronization as represented by low voltage, fast activity waves; the medial septal region projects to the hippocampal formation and there are projections from Ammon's horn back to the lateral septal region. There is no direct pathway, however, from the lateral septal area to the medial septal area. It has also been postulated that the output of hippocampal theta to the lateral septal

region and the subsequent suppression of Arousal System I is possible,but,this thesis does not rest on firm physiological grounds. Anatomical complexities such as Arousal System I and Arousal System II (Routtenberg,1967) are more relevant to the understanding of reward systems than they are for our purposes. Anatomically, the medial and lateral septal areas are probably richly interconnected but functionally, certain divisions of labour are quite evident.

Of particular relevance to this study is the distinction that Malmo (1964) drew between the effects of medial and lateral septal areas and heart rate - a decrease in heart rate alone is found with lateral septal stimulation while medial septal stimulation both increases and decreases heart rate and blood pressure. There also appears to be a question of priority of function within the septal area. Clody and Carlton (1969) restricted their septal lesions to the medial septal area and produced animals which were hyperplacid and were found to be consistently below normals in daily activity as measured by running wheel activity. It is probable that the medial septal area may affect temperament and motor activity but the neurophysiological details have yet to be worked out. The lateral septal area is mainly responsible for decreased autonomic activities because of its suppressing influence on the Reticular Activating System ; direct anatomical projections are not present in abundance but the major influences would likely be multisynaptic (Powell,1966). There also exist studies which strongly support a powerful subcortical influence on the reticular formation and it was Routtenberg (1967), more specifically, who maintained that the septal area suppresses the Reticular Activating System.This suppressing effect is supported by Kaada's results (1951). There is also evidence that

stimulation of the subcallosal and septal area induces a variety of events such as lowered heart rate, reduced respiratory movements and lowered blood pressure. Stimulation of the lateral septal area also causes pupils to be constricted. Thus, while substantial evidence for a subcortical suppressing influence on the RAS exists, the anatomical and physiological evidence does not as yet permit precise specification of the way in which this suppression is brought about, but the lateral septal area has definitely been strongly implicated.

Besides delineating the neurophysiological implications of this study, it is necessary to provide a proper conceptual framework to deal with the findings. Fried (1972) maintained that any unitary concept of the septal area has in the past been too simplistic to deal with this area of the brain which is so complex, neurologically speaking, and consequently multi-dimensional, functionally speaking. The present study was undertaken with the assumption that it is unlikely that the area itself makes a single, well-defined contribution to the physiology of emotional arousal. Though the results could be pursued further without referring to general theories of emotional arousal, we will now introduce such a theory. For, not only does the theory receive strong support from the data, but it is, in any case, one of the few theories sufficiently complex to make sense of the data. The theory in question is the hierarchal factor model proposed by Royce (1973), which may be graphically represented as follows:



Hierarchy of emotionality factors

(Royce,1973,p.328)

Based on higher-order factor analysis, the hierarchy is meant to convey more than taxonomic relations of class-inclusion. More specifically, the derivation of Anxiety and Motor Reactivity from the third order factor of generalized Emotional Reactivity is thought to indicate a multi-factor model for the release of emotional arousal. That is,

> the present model allows for two major second-order modes of expression via Motor Reactivity or Anxiety...The implication is that aroused energy (via the limbic system) is either externally released via the skeletal musculature (i.e. via first order factors of Acrophobia,Activity level, Audiogenic Reactivity, and Motor Discharge) ... or it is internalized via a disposition to Anxiety (i.e. via first order factors of Autonomic Balance and Territorial Marking) (Royce,1973,p.328)

Thus,Anxiety may be thought of as the internal'reverberation'

of emotional arousal which might also have been 'released' into the motor system. Moreover, it is hypothesized that the multi-modal (i.e. factor) release of aroused energy is controlled by (unknown) threshold variables which will prove crucial to an understanding of individual differences in emotionality (Royce,1973, p.373-375).

Other findings in the study may now be dealt with more briefly. Territoriality (IX) is the other first order factor under Anxiety and a slight increase is in fact recorded (see Figure 7) but it is not statistically significant. However, there is a significant lesion X sex interaction for this factor, bearing out previous findings that Territoriality is predominantly a male factor (Egan,Royce and Poley, 1973). This interaction is plotted in Fig. 5, making it clear that relative to the females in their own group septals do show a decrease in Territoriality, at least by comparison with normal controls.

There is little to be said about the results obtained on other factors. Acrophobia (III) is interpreted as fear of heights and is identified by the latency, time to descend and defecation measures of the pole apparatus. No significant differences were recorded but, it should be mentioned that startle reflexes by septals, especially in earlier trials, may have caused some spuriously low scores on the factor. There is a significant lesion X days interaction for this same factor. As is shown in Fig. 5, the habituation e effect which is found in both control groups does not occur with septals. In fact, scores on the earlier tests are lower than on later tests - though this, too, may be an artifact of the spetals' exaggerated startle reflex.

Tunneling 1 (V) is identified by elimination measures in tests involving passage through doorways and narrow passages, while Tunneling 2(XI) loads on the latency and activity measures of the same tests. While Cell and Hole-in-the-Wall were the only tests used in the present study (Table 1) neither of these invariant factors is considered to be experimentally dependent (Royce, 1973, p. 358), and it is reasonable to derive them, respectively, from the second order factors of Anxiety and Motor Reactivity. There were no significant differences for these factors, but the septal literature is plagued by effects which are both species-specific and situation-specific (c.f. Prosser, 1973), and the present results may simply reflect a further environmental selectivity on the process of arousal in septals. In other words, the more general and better verified pattern of decreased defecation and increased freezing which holds for septals in the open field and straightway, and which we have traced to a disruption at the second order, does not seem to hold for tunneling situations.

There is a final significant interaction which is worthy of mention. On Motor Discharge (II), lesioning has little effect on the emotionally disposed Balb strain by comparison with the less emotional C57 strain. This is compatible with the model offered above. Since the Balb strain already has a very low threshold for Motor Reactivity (see Royce, 1973, p. 360), there is little that the lesion can do to lower it further. On the other hand, a strong effect is noted for the C57 strain, which is normally highly resistant to this mode of emotional expression.

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Appendix

TABLES

	II	III	V	VIII	IX	XI
Open Field Latency	-62					
Open Field Activity	72					
Open Field Penetration	53					
Open Field Defecation				42	28	
Open Field Urination					30	
Straightway Latency	-41					
Straightway Activity	43	22				
Straightway Defecation				63		
Straightway Urination					50	
Pole Latency to leave top	63					
Pole Latency to descend	45	36				
Pole Defecation	70					
Pole Urination					38	
Cell Latency						39
Cell Defecation				26		
Cell Urination			56			
Hole-in-Wall Latency						48
Hole-in-Wall Defecation	20	31				
Hole-in-Wall Urination			22			

Table 1 Loadings greater than 20 on the six factors.

MOUSE #	SEX	STRAIN	% DAMAGE	PHOTOGRAPH AND DRAWING NUMBERS(SEE FIGS.8 & 9)
R002	Female	C57	75	1
R015	Female	Balb	60	2
R018	Female	Balb	71	3
R027	Female	C57	55	4
R035	Male	C57	70	5
R036	Male	C57	80	6
R037	Male	C57	72	7
R038	Male	C57	52	8
R042	Male	Balb	70	9
R046	Female	Balb	87	10
R047	Female	Balb	41	11
R054	Male	Balb	70	12
R059	Female	Balb	68	13
R064	Female	C57	75	14
R066	Female	C57	65	15
R078	Female	C57	66	16
R080	Male	Balb	72	17
R081	Male	Balb	46	18
R085	Male	Balb	83	19
R032	Male	C57	--	no picture taken

Table 2 Percentage volume of septum destroyed for each septal mouse brain.

TABLE 3

ANALYSIS OF VARIANCE TABLE FOR MOTOR DISCHARGE (FACTOR II)

SOURCE	SUM OF SQUARES	MEAN SQUARES	df	F VALUE
LESION	4286.93	2143.46	2	23.762 **
STRAIN	4812.84	4812.84	1	53.354 **
LESION X STRAIN	589.62	294.81	2	3.268 *
SEX	72.49	72.49	1	0.804
LESION X SEX	126.119	63.09	2	0.699
SEX X STRAIN	0.55	0.55	1	0.006
LESION X SEX X STRAIN	75.18	37.59	2	0.417
ERROR (a)	4329.87	90.21	48	
DAYS	824.88	206.22	4	4.947 **
DAYS X LESION	435.63	54.45	8	1.306
DAYS X STRAIN	283.53	70.88	4	1.701
DAYS X LESION X STRAIN	64.11	8.01	8	0.192
DAYS X SEX	200.70	50.18	4	1.204
DAYS X LESION X SEX	318.82	39.85	8	0.856
DAYS X STRAIN X SEX	124.16	31.04	4	0.745
DAYS X LESION X SEX X STRAIN	554.16	69.27	8	1.662
ERROR (b)	8003.12	41.68	192	

** significant at .01 level of significance;

* significant at .05 level of significance

TABLE 4

ANALYSIS OF VARIANCE TABLE FOR ACROPHOBIA (FACTOR III)

SOURCE	SUM OF SQUARES	MEAN SQUARES	df	F VALUE
LESION	278.61	139.31	2	0.681
STRAIN	65.97	65.97	1	0.323
LESION X STRAIN	441.79	220.90	2	1.081
SEX	20.04	20.04	1	0.098
LESION X SEX	434.19	217.10	2	1.062
SEX X STRAIN	99.46	99.46	1	0.487
LESION X STRAIN X SEX	510.03	255.02	2	1.248
ERROR (a)	9812.28	204.42	48	
DAYS	1509.80	377.45	4	6.270 **
DAYS X LESION	1665.55	208.19	8	3.459 **
DAYS X STRAIN	152.50	38.10	4	0.633
DAYS X LESION X STRAIN	1326.04	165.76	8	2.753 **
DAYS X SEX	131.34	32.83	4	0.545
DAYS X LESION X SEX	746.56	93.32	8	1.550
DAYS X SEX X STRAIN	153.83	38.46	4	0.638
DAYS X LESION X SEX X STRAIN	1094.11	136.76	8	2.272
ERROR (b)	11558.02	60.20	192	

** significant at .01 level of significance;

* significant at .85 level of significance.

TABLE 5

ANALYSIS OF VARIANCE TABLE FOR TUNNELING I (FACTOR V)

SOURCE	SUM OF SQUARES	MEAN SQUARES	df	F VALUE
LESION	205.51 102.76	102.76	2	1.060
STRAIN	42.52	42.52	1	0.439
LESION X STRAIN	994.47	496.24	2	5.129 **
SEX	170.67	170167	1	1.760
LESION X SEX	239.60	119.80	2	1.236
SEX X STRAIN	104.74	104.74	1	1.080
LESION X SEX X STRAIN	111.14	55.57	2	0.573
ERROR (a)	4653.43	96.95	48	
DAYS	1617.11	404.28	4	5.807 **
DAYS X LESION	557.09	69.64	8	1.000
DAYS X STRAIN	399.19	99.80	4	1.433
DAYS X LESION X STRAIN	413.97	51.75	8	0.743
DAYS X SEX	517.33	129.33	4	1.858
DAYS X LESION X SEX	831.37	103.92	8	1.493
DAYS X SEX X STRAIN	69.20	17.30	4	0.248
DAYS X LESION X SEX X STRAIN	2464.88	308.11	8	4.426
ERROR (b)	13367.10	69.62	192	

** significant at .01 level of significance;

* significant at .05 level of significance.

TABLE 6

ANALYSIS OF VARIANCE TABLE FOR AUTONOMIC BALANCE (FACTOR VIII)

SOURCE	SUM OF SQUARES	MEAN SQUARES	df	F VALUE
LESION	2989.83	1494.92	2	8.957 **
STRAIN	2185.54	2185.54	1	13.096 **
LESION X STRAIN	456.28	228.14	2	1.367
SEX	615.26	615.26	1	3.687
LESION X SEX	490.58	245.29	2	1.470
SEX X STRAIN	0.27	0.27	1	0.002
LESION X SEX X STRAIN	264.22	132.11	2	0.792
ERROR (a)	8010.75	48		
DAYS	882.36	220.59	4	3.797 **
DAYS X LESION	240.37	30.05	8	0.517
DAYS X STRAIN	397.04	99.26	4	1.708
DAYS X LESION X STRAIN	745.22	93.15	8	1.603
DAYS X SEX	287.99	72.00	4	1.239
DAYS X LESION X SEX	304.32	38.04	8	0.655
DAYS X SEX X STRAIN	85.30	21.32	4	0.367
DAYS X LESION X SEX X STRAIN	889.51	111.19	8	1.914
ERROR (b)	11155.08	58.10	192	

** significant at .01 level of significance;

* significant at .05 level of significance.

TABLE 7

ANALYSIS OF VARIANCE TABLE FOR TERRITORIALITY (FACTOR EX)

SOURCE	SUM OF SQUARES	MEAN SQUARES	df	F VALUE
LESION	154.80	77.40	2	0.807
STRAIN	68.05	68.05	1	0.710
LESION X STRAIN	407.74	203.87	2	2.127
SEX	958.15	958.15	1	9.995 **
LESION X SEX	750.94	375.47	2	3.917 *
SEX X STRAIN	59.41	59.41	1	0.620
LESION X STRAIN X SEX	52.71	26.36	2	0.275
	4601.58			
ERROR (a)	4601.58	95.87		
DAYS	630.11	157.53	4	1.657
DAYS X LESION	831.16	103.89	8	1.093
DAYS X STRAIN	425.34	106.33	4	1.119
DAYS X LESION X STRAIN	1184.59	148.07	8	1.558
DAYS X SEX	433.66	108.42	4	1.141
DAYS X LESION X SEX	720.69	90.09	8	0.948
DAYS X SEX X STRAIN	188.73	47.18	4	0.496
DAYS X LESION X SEX X STRAIN	282.28	35.28	8	0.371
ERROR (b)	18250.06	95.05	192	

** significant at .01 level of significance;

* significant at .05 level of significance.

TABLE 8

ANALYSIS OF VARIANCE TABLE FOR TUNNELING 2 (FACTOR XI)

SOURCE	SUM OF SQUARES	MEAN SQUARES	df	F VALUE
LESION	665.87	332.94	2	1.868
STRAIN	6.53	6.53	1	0.037
LESION X STRAIN	128.11	64.05	2	0.359
SEX	11.93	11.93	1	0.067
LESION X SEX	65.91	32.96	2	0.185
SEX X STRAIN	136.39	136.39	1	0.765
LESION X SEX X STRAIN	158.02	79.01	2	0.443
ERROR (a)	8554.47	178.22		
DAYS	1114.47	278.62	4	3.601 **
DAYS X LESION	948.33	118.54	8	1.532
DAYS X STRAIN	124.68	31.17	4	0.403
DAYS X LESION X STRAIN	513.51	64.19	8	0.830
DAYS X SEX	295.64	73.91	4	0.955
DAYS X LESION X SEX	562.28	70.28	8	0.908
DAYS X SEX X STRAIN	423.75	105.94	4	1.369
DAYS X LESION X SEX X STRAIN	1433.55	179.19	8	2.316 **
ERROR (b)	14856.68	77.38	192	

** significant at .01 level of significance;

* significant at .05 level of significance.

TABLE 9

TABLE OF FACTOR SCORES FOR
ALL SIGNIFICANT MAIN AND
INTERACTION EFFECTS

MOTOR DISCHARGE (FACTOR II)

Main Effects

Lesion Type:	Control	Operate Control	Septal
	51.42	53.34	44.54

Strain:	C57	Balb
	53.77	45.76

Over-all Trend (Days):	Day 1	Day 2	Day 3	Day 4	Day 5
	52.94	49.89	48.74	48.70	48.56

Lesion X Strain Interaction

	Control	Operate Control	Septal
C57	56.01	58.70	46.61
Balb	46.84	47.98	42.46

ACROPHOBIA (FACTOR III)

Main Effects

Over-all Trend (Days):	Day 1	Day 2	Day 3	Day 4	Day 5
	51.37	53.18	49.60	49.42	46.44

Lesion X Day Interaction

	Day 1	Day 2	Day 3	Day 4	Day 5
Control	53.95	56.59	48.39	48.71	42.42
Operate Control	53.13	52.30	50.88	52.16	48.32
Septal	47.02	50.65	49.53	50.38	48.58

TABLE 9 (CONTINUED)

TUNNELING 1 (FACTOR V)

Main Effects

Over-all Trend (Days):	Day 1	Day 2	Day 3	Day 4	Day 5
	53.94	50.55	48.89	48.45	47.23

Strain X Lesion Interaction

	Control	Operate Control	Septal
C57	48.22	49.02	53.32
Balb	51.87	48.38	48.06

AUTONOMIC BALANCE (FACTOR VIII)

Main Effects

Lesion TYpe:	Control	Operate Control	Septal
	53.33	50.91	45.76

Strain:	C57	Balb
	47.30	52.70

Over-all Trend (Days):	Day 1	Day 2	Day 3	Day 4	Day 5
	50.86	52.08	47.55	48.42	51.08

TERRITORIALITY (FACTOR IX)

Main Effects

Sex:	Male	Female
	51.79	48.21

Lesion X Sex Interaction

	Male	Female
Control	54.55	46.49
Operate Control	51.18	49.82
Septal	49.64	48.33

TUNNELING 2 (FACTOR XI)

Main Effects

Over-all Trend (Days)	Day 1	Day 2	Day 3	Day 4	Day 5
	53.42	50.48	49.55	47.76	48.80

TABLE 10

FACTOR SCORES FOR EMOTIONALITY PROFILE FOR LESION TYPE

FACTOR	MEAN SCORE FOR CONTROL GROUP	MEAN SCORE FOR OPERATE CONTROL GROUP	MEAN SCORE FOR SEPTAL GROUP
II	51.42	53.34	44.54
III	49.41	51.36	49.23
V	50.04	48.70	50.69
VIII	53.333	50.91	45.76
IX	50.52	50.50	48.98
XI	49.96	48.19	51.84

TABLE 11

FACTOR SCORES OF EACH CELL FOR EACH FACTOR OVER 5 DAYS
(EACH CELL REPRESENTS ONE TREATMENT COMBINATION OF
LESION TYPE,STRAIN AND SEX. N= 5)

MOTOR DISCHARGE
FACTOR II

LESION TYPE	STRAIN	SEX	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
OPERATE CONTROL	C57	MALE	63.43	61.30	57.57	60.00	57.64
OPERATE CONTROL	C57	FEMALE	61.42	58.83	56.54	56.43	53.80
OPERATE CONTROL	BALB	MALE	50.83	47.20	48.20	47.39	48.60
OPERATE CONTROL	BALB	FEMALE	50.06	49.99	43.20	47.45	46.94
CONTROL	C57	MALE	58.54	56.99	55.99	55.71	52.59
CONTROL	C57	FEMALE	56.23	58.88	55.08	54.08	56.01
CONTROL	BALB	MALE	44.52	46.55	42.25	47.50	49.28
CONTROL	BALB	FEMALE	50.27	53.27	47.18	47.53	49.93
SEPTAL	C57	MALE	48.96	42.70	48.55	48.65	45.97
SEPTAL	C57	FEMALE	57.31	51.58	44.45	38.05	39.89
SEPTAL	Balb	MALE	50.77	40.79	42.58	53.25	43.36
SEPTAL	Balb	FEMALE	42.98	40.48	43.27	38.42	38.74

TABLE 11 (CONTINUED)

FACTOR SCORES OF EACH CELL FOR EACH FACTOR OVER 5 DAYS
(EACH CELL REPRESENTS ONE TREATMENT COMBINATION OF
LESION TYPE,STRAIN AND SEX. N= 5)

ACROPHOBIA
FACTOR III

LESION TYPE	STRAIN	SEX	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
OPERATE CONTROL	C57	MALE	51.07	52.18	52.67	54.75	50.03
OPERATE CONTROL	C57	FEMALE	56.57	55.21	47.80	50.98	44.61
OPERATE CONTROL	BALB	MALE	54.76	52.94	54.13	53.91	54.09
OPERATE CONTROL	BALB	FEMALE	50.12	48.89	48.90	49.00	44.54
CONTROL	C57	MALE	48.32	49.24	49.10	44.19	45.23
CONTROL	C57	FEMALE	44.78	57.62	48.54	45.64	39.71
CONTROL	BALB	MALE	51.98	62.27	46.70	45.73	38.87
CONTROL	BALB	FEMALE	70.72	57.24	49.23	47.26	45.87
SEPTAL	C57	MALE	51.62	51.35	49.48	45.74	43.24
SEPTAL	C57	FEMALE	48.89	48.36	50.68	48.72	59.61
SEPTAL	BALB	MALE	46.95	51.65	53.22	56.34	46.00
SEPTAL	BALB	FEMALE	40.61	51.22	44.73	50.71	45.48

TABLE 11 (CONTINUED)

FACTOR SCORES OF EACH CELL FOR EACH FACTOR OVER 5 DAYS
(EACH CELL REPRESENTS ONE TREATMENT COMBINATION OF
LESION TYPE,STRAIN AND SEX. N= 5)

TUNNELING I
FACTOR V

LESION TYPE	STRAIN	SEX	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
OPERATE CONTROL	C57	MALE	43.40	43.95	54.74	48.75	44.53
OPERATE CONTROL	C57	FEMALE	59.84	49.42	47.88	48.32	49.42
OPERATE CONTROL	BALB	MALE	62.26	46.32	47.83	45.11	45.10
OPERATE CONTROL	BALB	FEMALE	45.72	46.31	47.73	50.67	46.73
CONTROL	C57	MALE	58.31	50.61	43.80	47.13	48.26
CONTROL	C57	FEMALE	42.01	45.78	50.73	48.78	47.74
CONTROL	BALB	MALE	53.78	63.78	53.80	47.43	48.57
CONTROL	BALB	FEMALE	60.82	47.96	48.74	43.92	49.87
SEPTAL	C57	MALE	54.20	63.89	49.10	59.47	45.12
SEPTAL	C57	FEMALE	55.64	52.66	49.01	48.75	55.38
SEPTAL	BALB	MALE	55.50	50.93	47.44	50.33	43.50
SEPTAL	BALB	FEMALE	55.78	44.95	45.92	42.74	43.47

TABLE 11(CONTINUED)

FACTOR SCORES OF EACH CELL FOR EACH FACTOR OVER 5 DAYS (EACH CELL REPRESENTS ONE TREATMENT COMBINATION OF LESION TYPE, STRAIN AND SEX. N = 5)

AUTONOMIC BALANCE
FACTOR VIII

LESION TYPE	STRAIN	SEX	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
OPERATE CONTROL	C57	MALE	52.98	46.73	41.55	42.60	50.99
OPERATE CONTROL	C57	FEMALE	40.66	48.23	47.50	46.89	49.58
OPERATE CONTROL	BALB	MALE	50.24	61.03	51.15	53.88	57.83
OPERATE CONTROL	BALB	FEMALE	53.99	58.68	49.09	50.61	55.97
CONTROL	C57	MALE	57.32	59.61	51.03	57.34	49.74
CONTROL	C57	FEMALE	47.51	43.65	44.70	46.88	47.22
CONTROL	BALB	MALE	59.88	57.66	57.01	52.43	63.47
CONTROL	BALB	FEMALE	49.47	57.53	54.34	56.53	53.42
SEPTAL	C57	MALE	39.38	44.47	45.59	45.10	46.12
SEPTAL	C57	FEMALE	44.45	47.80	40.84	47.87	44.73
SEPTAL	BALB	MALE	54.10	53.77	42.32	39.72	49.95
SEPTAL	BALB	FEMALE	52.34	45.83	45.54	41.35	43.97

TABLE 11(CONTINUED)

FACTOR SCORES OF EACH CELL FOR EACH FACTOR OVER 5 DAYS (EACH CELL REPRESENTS ONE TREATMENT COMBINATION OF LESION TYPE, STRAIN AND SEX. N = 5)

TERRITORIALITY
FACTOR IX

LESION TYPE	STRAIN	SEX	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
OPERATE CONTROL	C57	MALE	58.36	53.93	51.55	45.24	45.12
OPERATE CONTROL	C57	FEMALE	49.65	43.82	49.44	46.12	49.51
OPERATE CONTROL	BALB	MALE	56.56	48.75	53.70	46.61	52.01
OPERATE CONTROL	BALB	FEMALE	50.75	46.44	57.71	52.59	52.13
CONTROL	C57	MALE	61.34	46.97	51.89	56.56	48.49
CONTROL	C57	FEMALE	44.94	44.73	43.67	46.24	46.61
CONTROL	BALB	MALE	57.05	56.02	57.62	50.36	59.12
CONTROL	BALB	FEMALE	40.92	52.22	53.63	45.46	46.49
SEPTAL	C57	MALE	49.82	58.16	45.78	53.50	49.65
SEPTAL	C57	FEMALE	50.85	46.31	45.71	55.60	46.18
SEPTAL	BALB	MALE	56.17	46.66	45.46	45.69	45.50
SEPTAL	BALB	FEMALE	56.95	46.11	44.76	45.00	45.84

TABLE 11(CONTINUED)

FACTOR SCORES OF EACH CELL FOR EACH FACTOR OVER 5 DAYS
(EACH CELL REPRESENTS ONE TREATMENT COMBINATION OF
LESION TYPE, STRAIN AND SEX. N =5)

TUNNELING 2
FACTOR XI

LESION TYPE	STRAIN	SEX	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
OPERATE CONTROL	C57	MALE	51.00	44.78	48.81	49.09	48.32
OPERATE CONTROL	C57	FEMALE	55.17	48.58	51.62	48.51	45.96
OPERATE CONTROL	BALB	MALE	52.38	48.91	47.71	51.06	48.41
OPERATE CONTROL	BALB	FEMALE	42.16	42.71	42.56	46.54	49.62
CONTROL	C57	MALE	55.82	49.60	46.74	49.56	45.54
CONTROL	C57	FEMALE	45.54	49.41	54.22	48.45	48.71
CONTROL	BALB	MALE	51.51	58,15	47.91	46.92	47.64
CONTROL	BALB	FEMALE	54.25	48.01	48.93	49.18	53.20
SEPTAL	C57	MALE	49.50	55.96	52.06	53.62	44.70
SEPTAL	C57	FEMALE	65.96	57.99	47.21	39.23	52.79
SEPTAL	BALB	MALE	61.50	51.88	49.49	45.41	52.03
SEPTAL	BALB	FEMALE	56.21	49.75	57.38	45.53	48.66

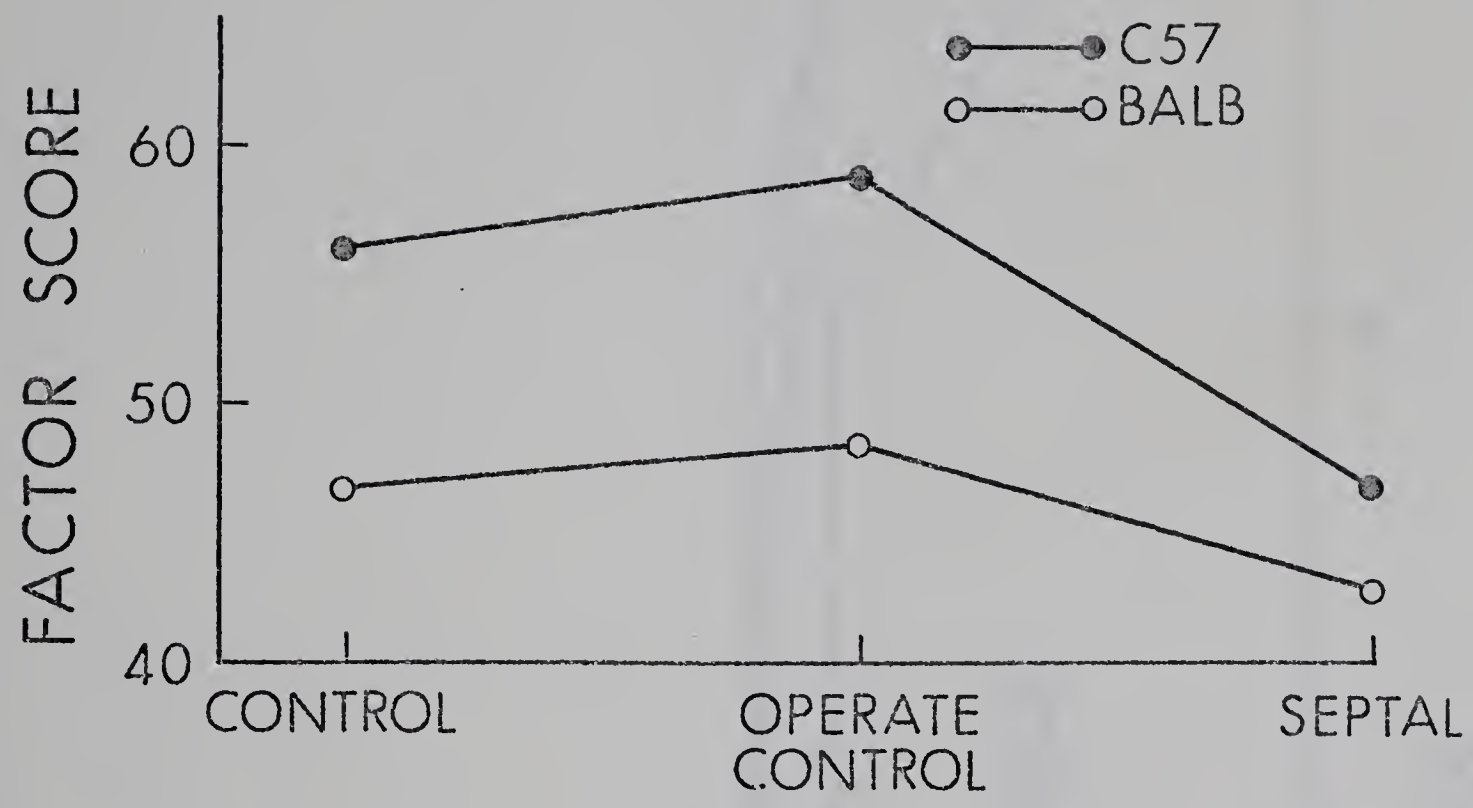


Figure 1. Two-way interaction between lesion and strain for Factor II (Motor Discharge)

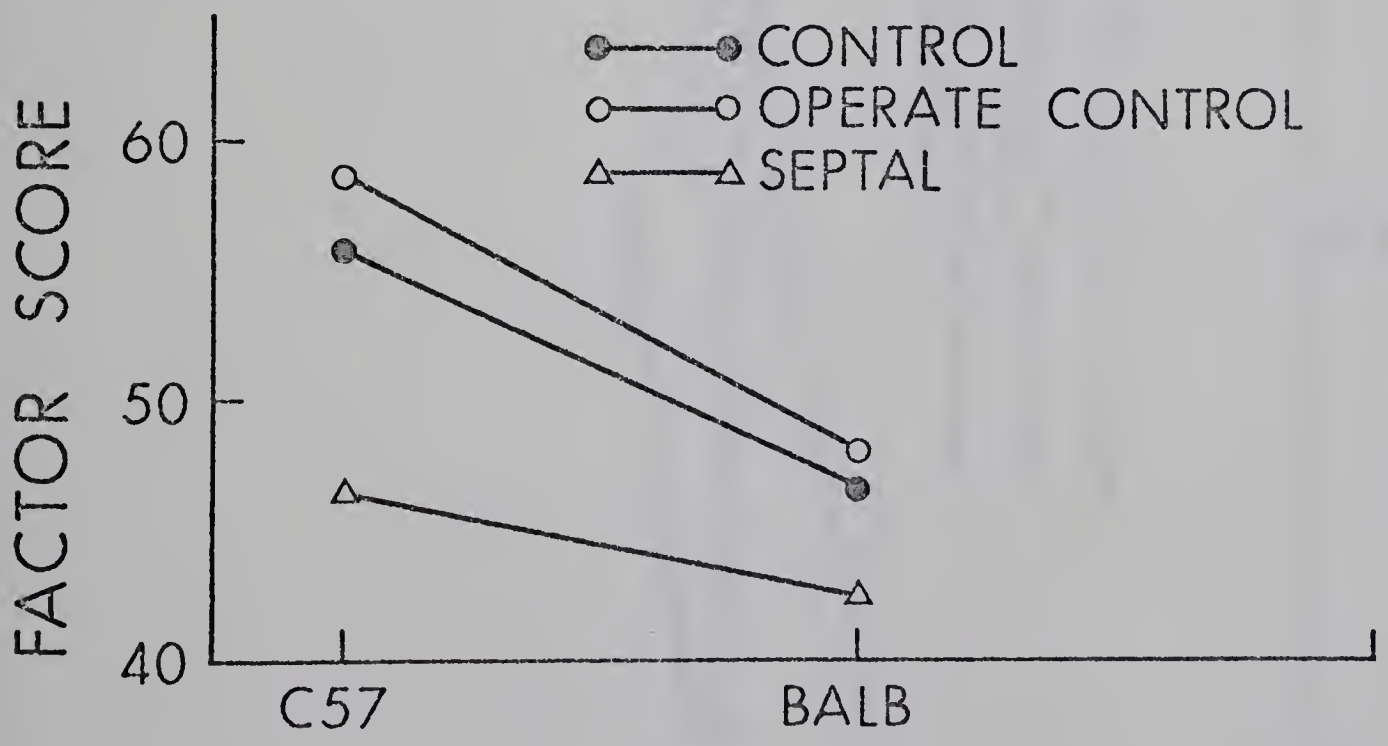


Figure 2. Two-way interaction between lesion and strain for Factor II (Motor Discharge).

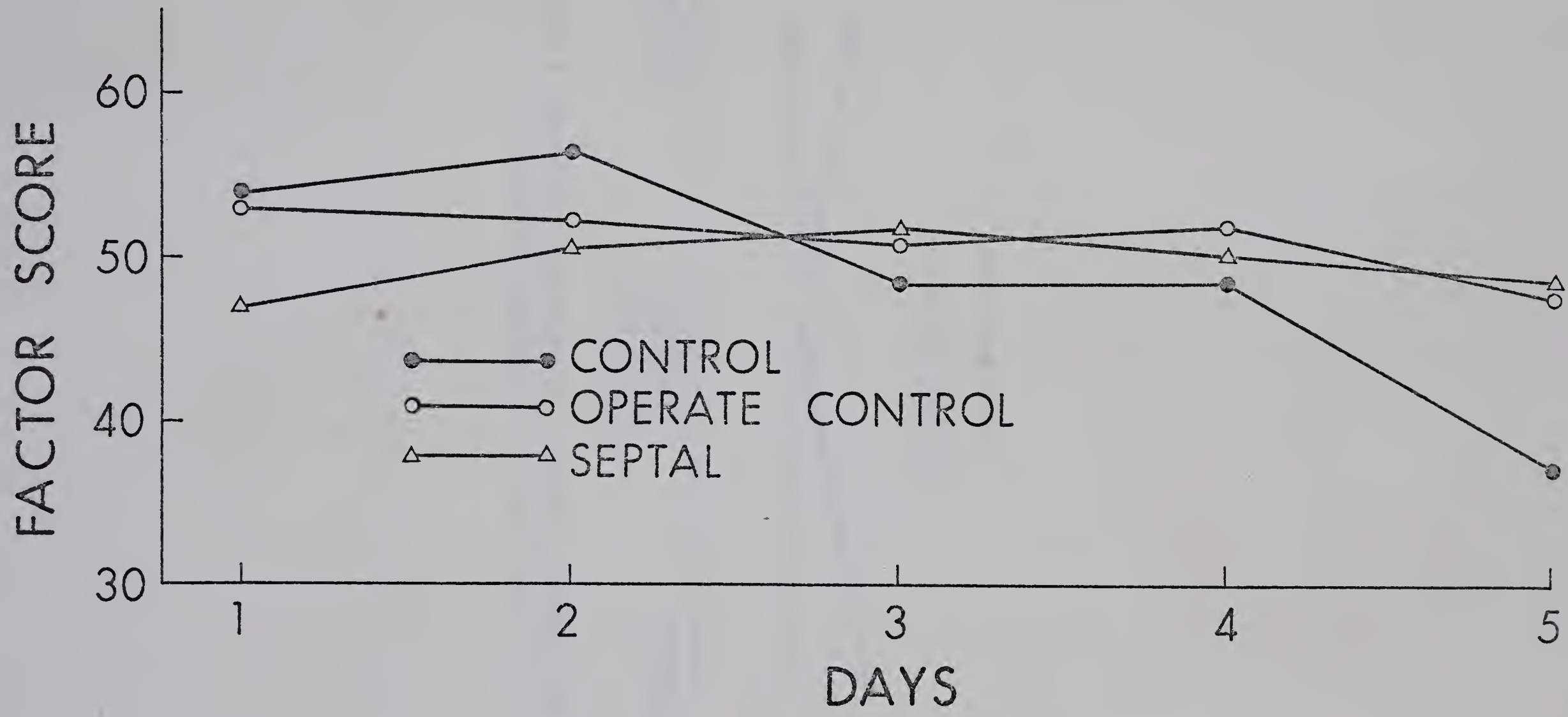


Figure 3. Two-way interaction between lesion and days for Factor III (Acrophobia).

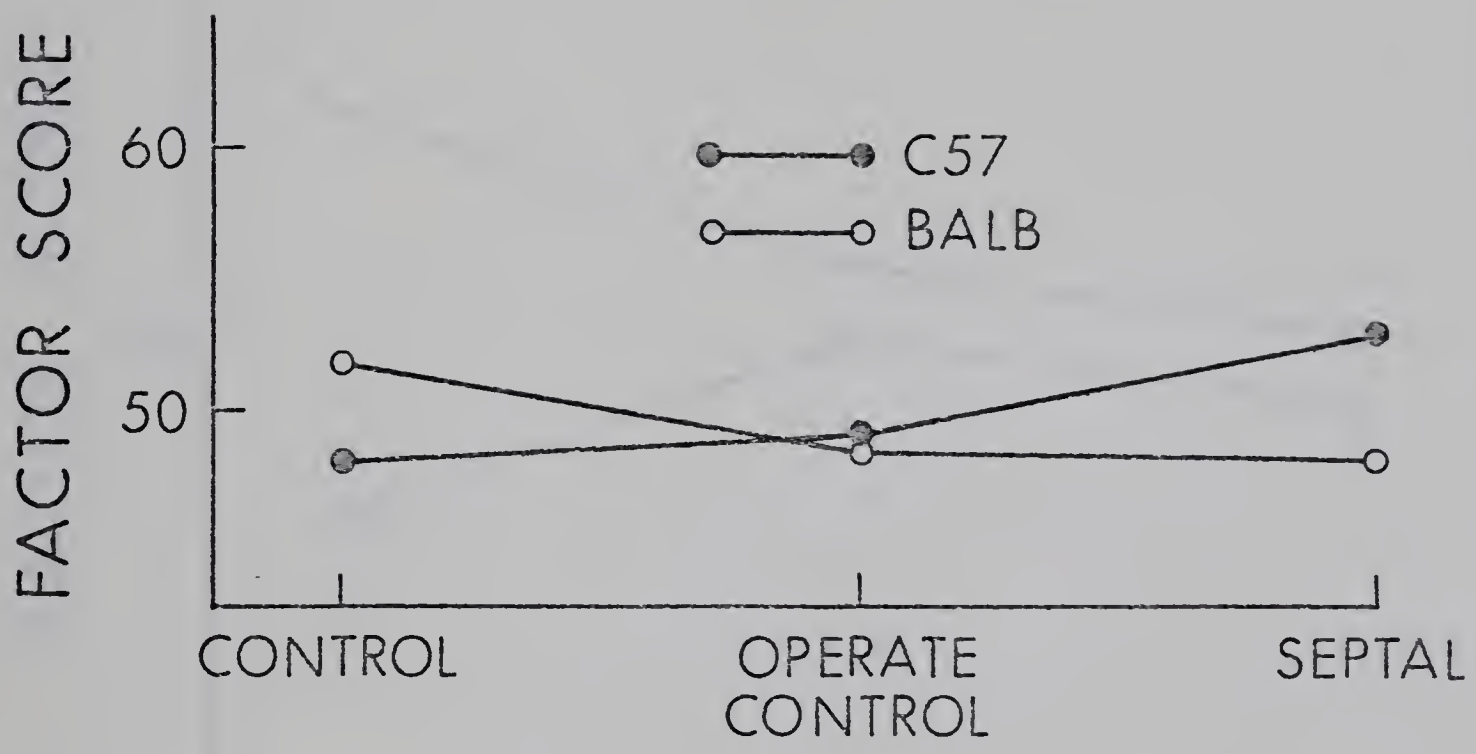


Figure 4. Two-way interaction between lesion and strain for Factor V (Tunneling 1).

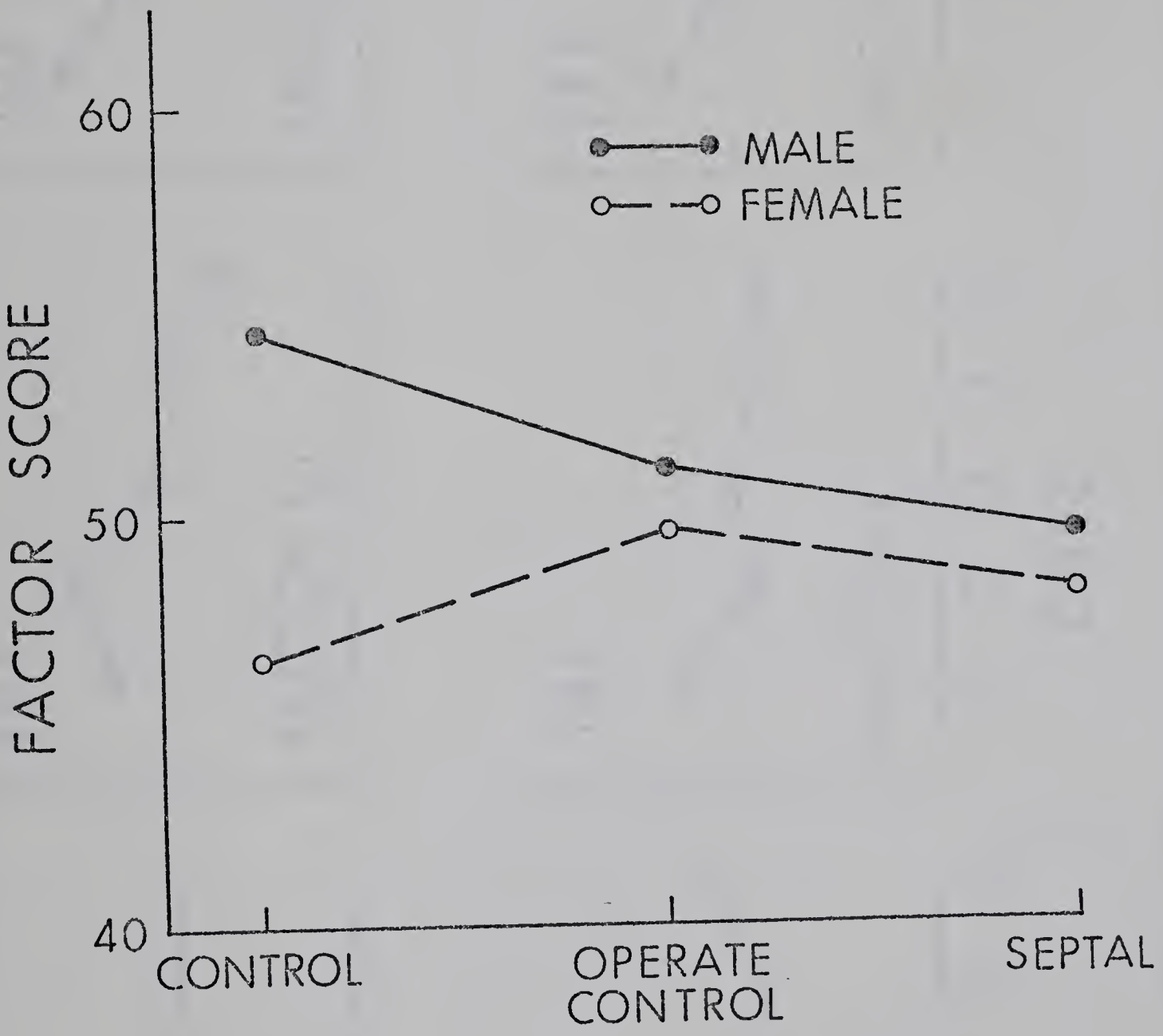
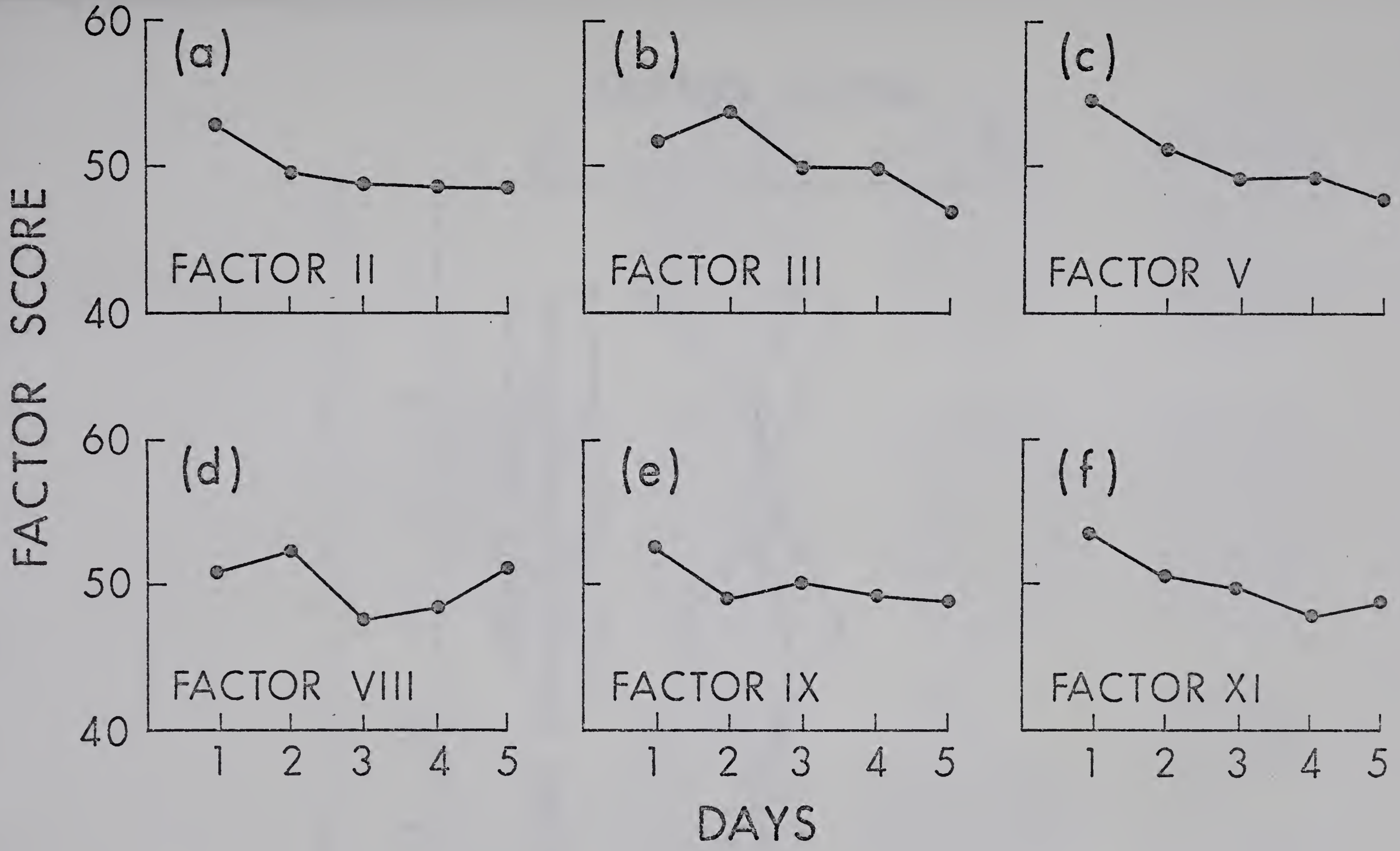


Figure 5. Two-way interaction between lesion and sex for Factor IX (Territoriality).



Figures 6a to 6f. Mean factor scores averaged over levels of sex and strain for each of the days. This overall trend is plotted separately for each factor.

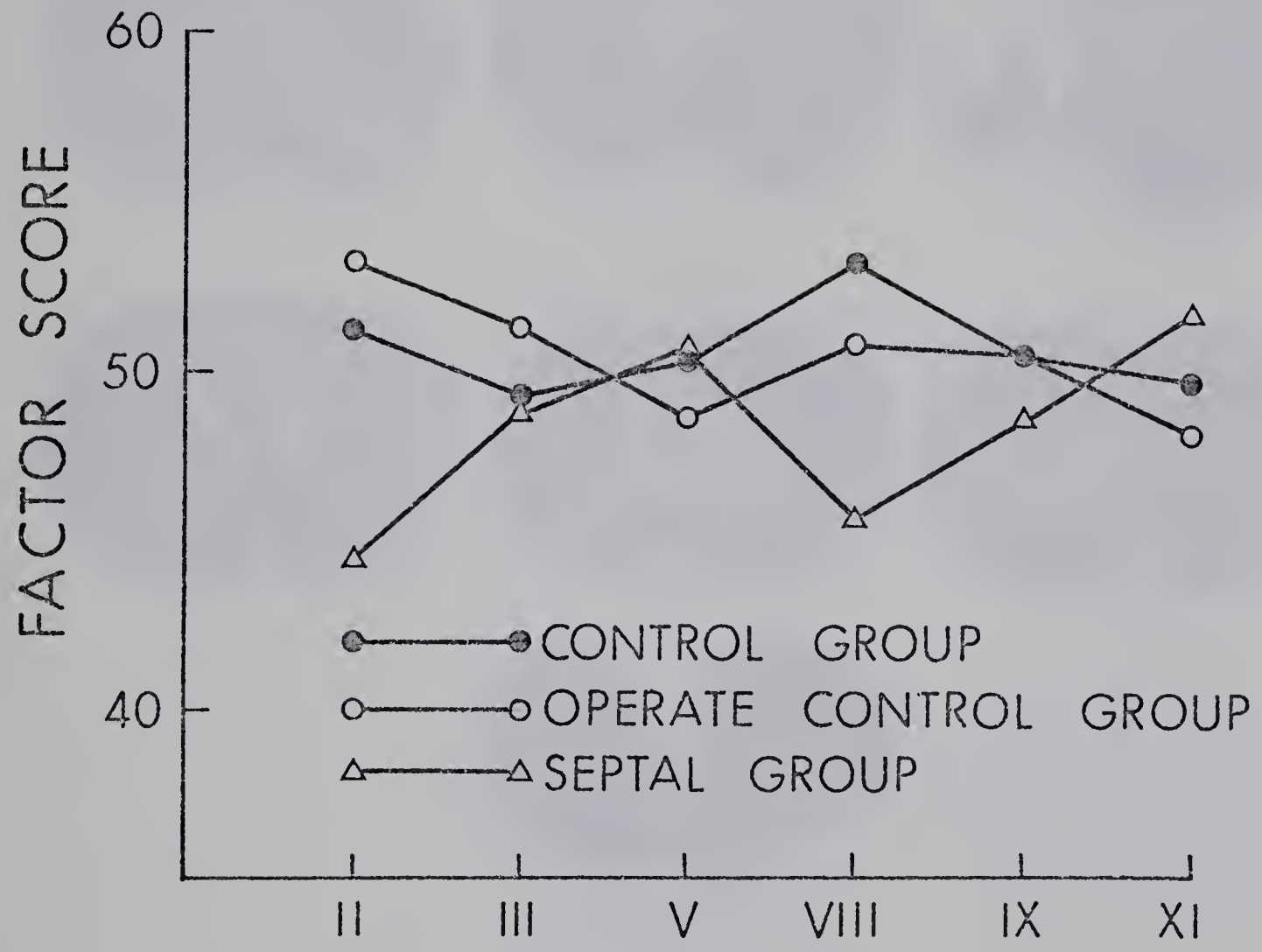


Figure 7. Emotionality profiles for three lesion types.

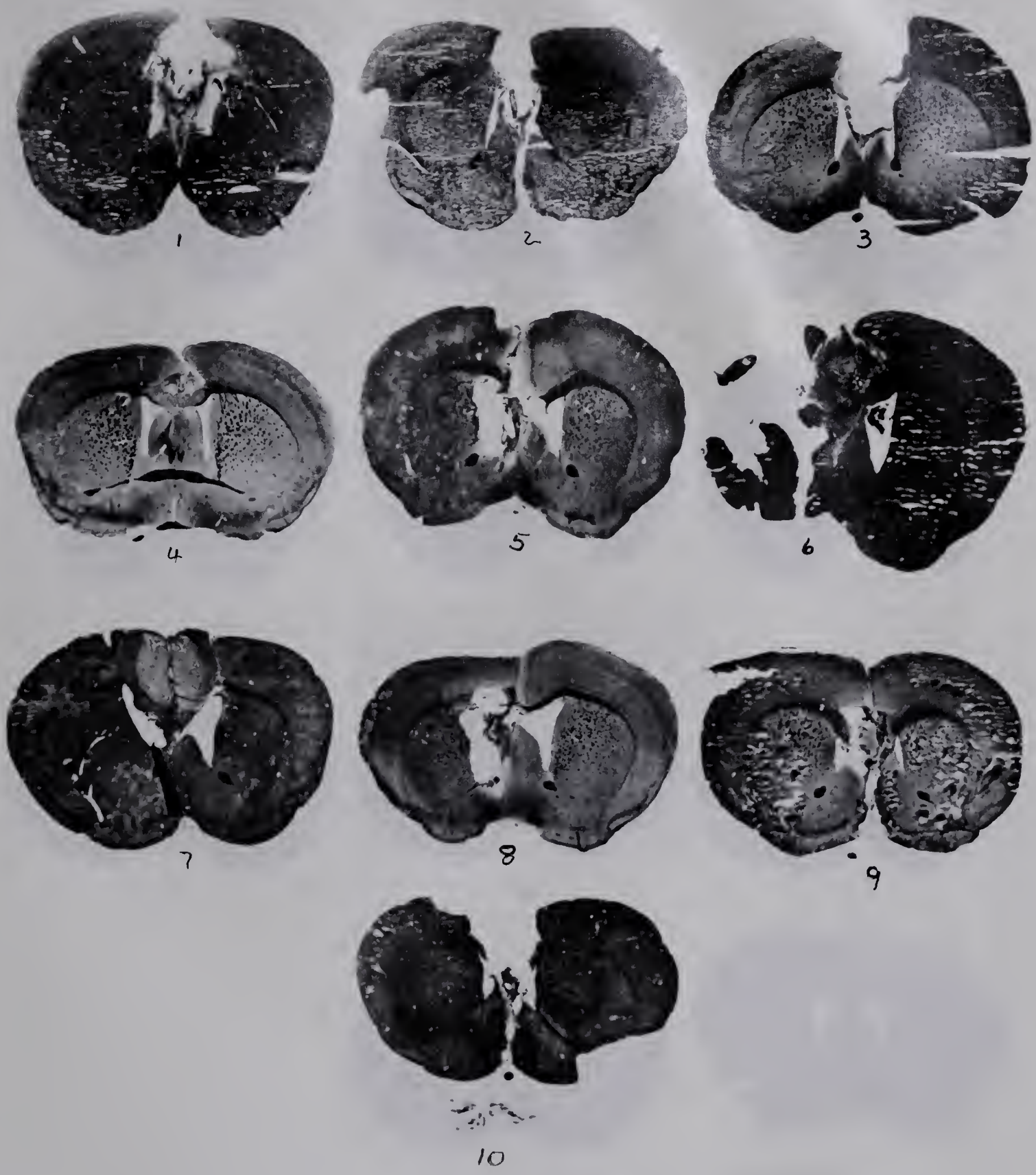


Figure 8: Photographs of cross-sectional view of cortical lesion for each mouse brain. (See text, page 13 , for more details.)

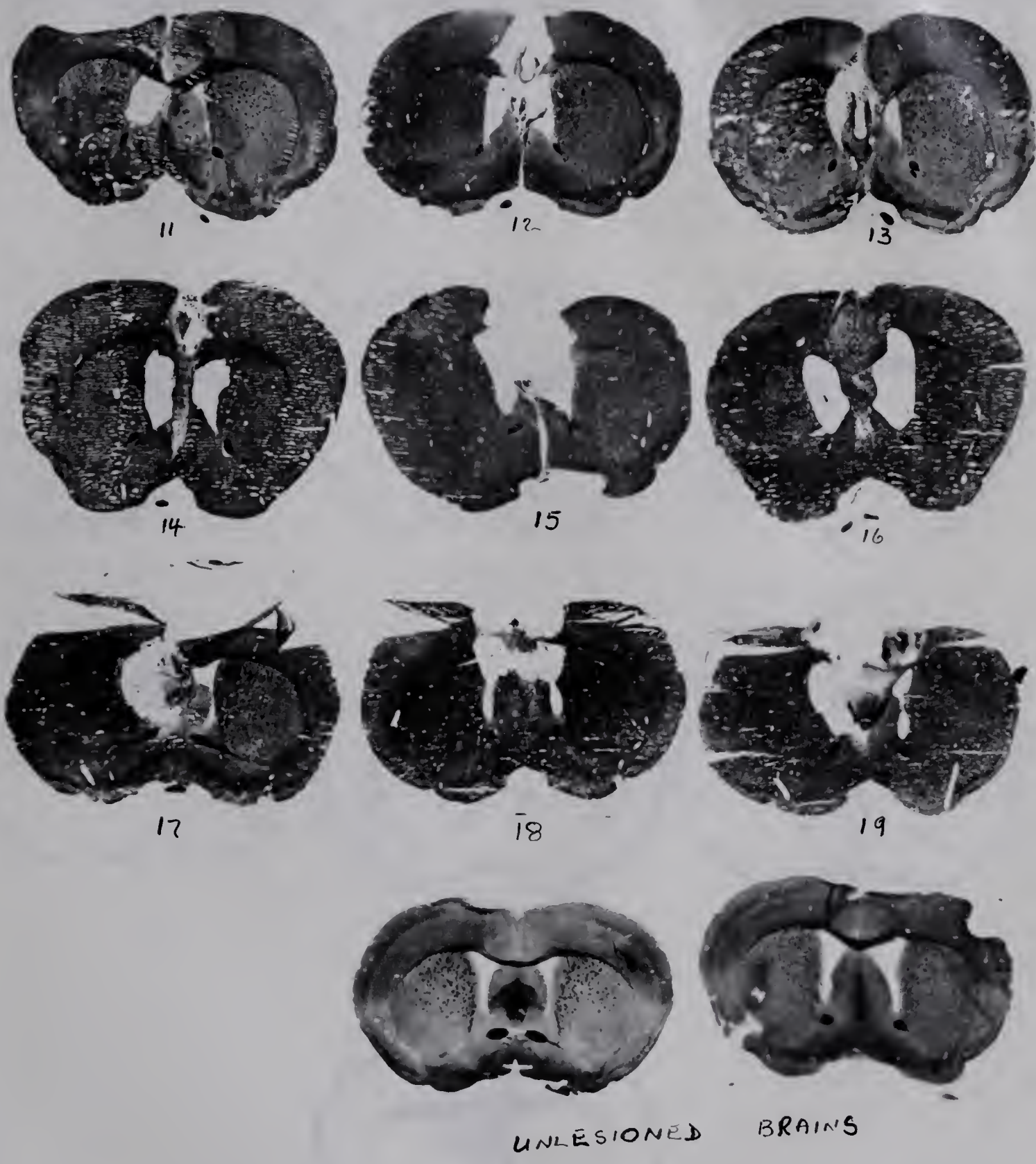
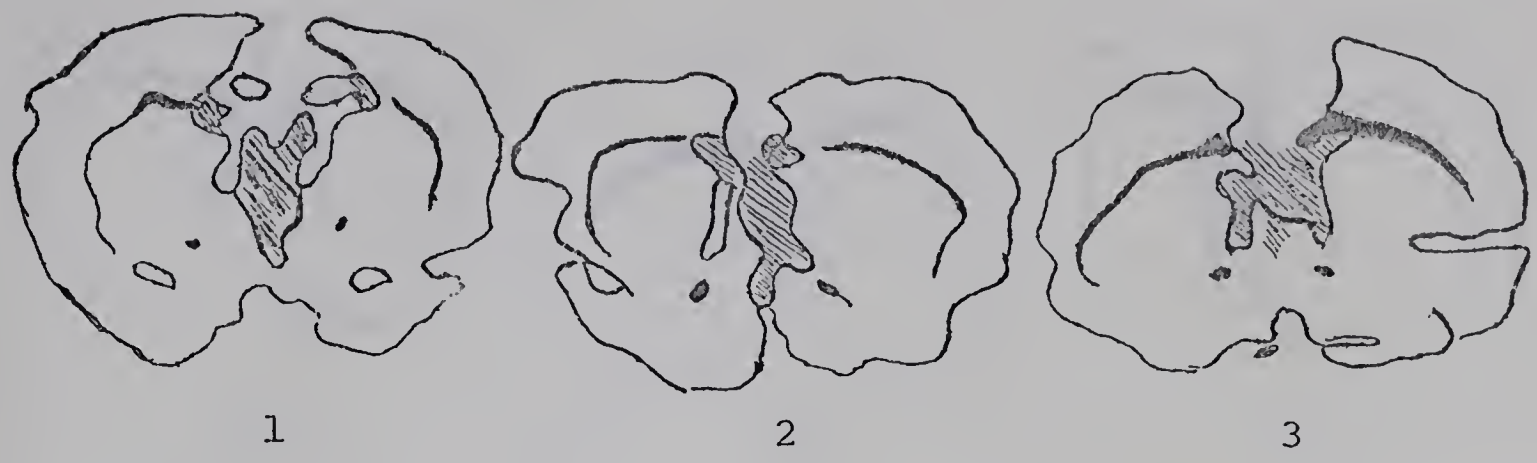


Figure 8. (continued).



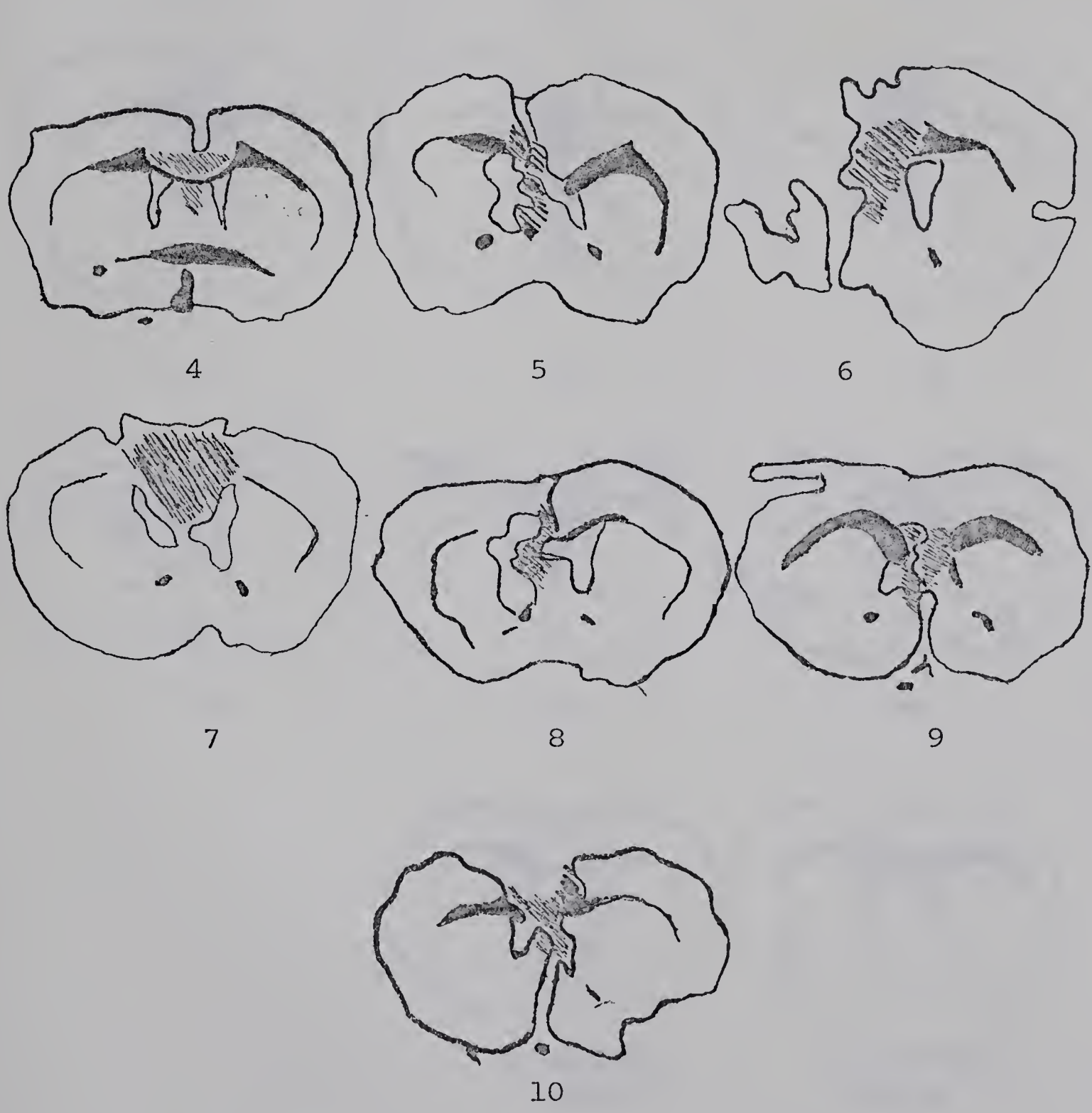


Figure 9. Schematic drawings of cross-sectional view of each mouse brain. Shaded area represents area of septal damage. Refer to Table 2 and text p. 13.

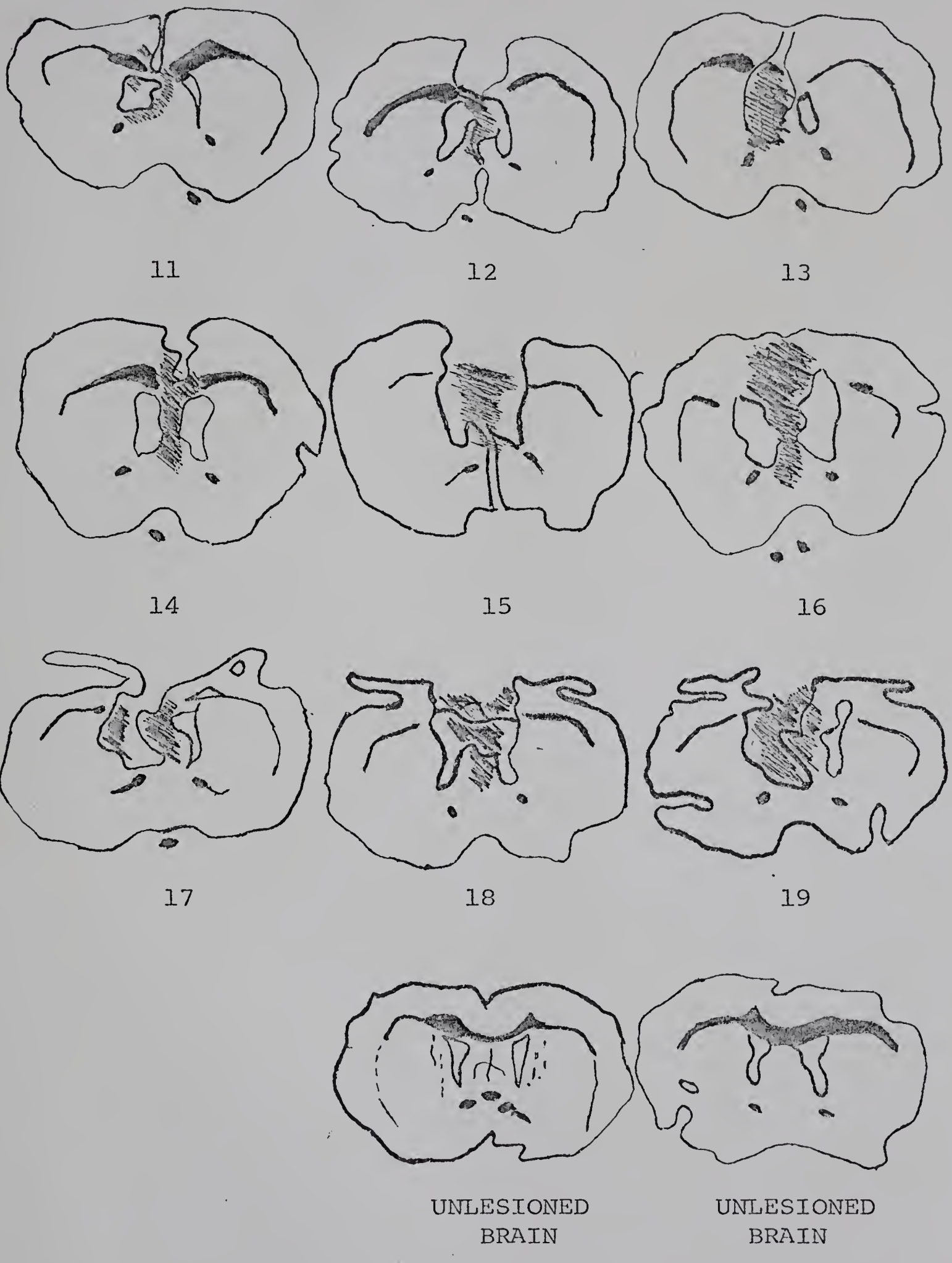


Figure 9. Schematic drawings of cross-sectional view of each mouse brain. Shaded area represents area of septal damage. Refer to Table 2 and text p.13.